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Management and Conservation Article

Evidence of a Minimum Patch Size Threshold of Reproductive Success in an Endangered Songbird

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ABSTRACT That area-sensitive songbirds breed only in relatively large patches suggests that there may be a minimum patch size threshold in which they will breed, even when controlling for the total amount of habitat in the landscape. We searched for minimum patch size thresholds of presence, territory establishment by males, pairing success, and reproductive success for 2 migratory songbirds that differed in sensitivity to patch size: golden-cheeked warblers (*Dendroica chrysoparia*) and white-eyed vireos (*Vireo griseus*). We assessed 2 potential limiting factors: brown-headed cowbird (*Molothrus ater*) parasitism and arthropod biomass (food resource). We determined whether either factor was related to patch size and compared measurements of each above and below the observed thresholds. We monitored 24 golden-cheeked warbler and 47 white-eyed vireo territories in 12 patches. We found evidence of a minimum patch size threshold (between 15.0 ha and 20.1 ha) of reproductive success for golden-cheeked warblers, but not for white-eyed vireos. We found no minimum patch size thresholds for presence, territory establishment by males, or pair formation for either species. Conservation practices based on thresholds of presence, territory establishment, or pair formation might not address issues of reproduction for golden-cheeked warblers. We failed to find evidence that cowbird parasitism or arthropod biomass were limiting factors. The ability to identify patch size thresholds of reproductive success for target species could be useful in conservation and management for setting goals for retention and restoration of target species' habitat patch size.

KEY WORDS arthropods, brown-headed cowbird, forest stand, forest tract, golden-cheeked warbler, thresholds, white-eyed vireo, woodlot.

The concept of ecological thresholds, defined as points or zones at which relatively rapid change occurs from one condition to another (Huggett 2005), has pervaded ecology in various forms. Ecological thresholds are fundamental to Shelford's law of tolerance (Shelford 1931), carrying capacity (Ricker 1954), and nonequilibrium paradigms of vegetation dynamics (Briske et al. 2003). Ecological thresholds also play a role in distribution and abundance of species in relation to landscape structure (With and Crist 1995, Jansson and Angelstam 1999). For example, empirical evidence shows that there are maximum distances between patches that some species will cross (Radford and Bennett 2004, van der Ree et al. 2004, Denoël and Ficetola 2007). Ecological thresholds may also play a role in the distribution and abundance of area-sensitive species (those that are found less often in small than large forest fragments; Zanette et al. 2000). Many area-sensitive songbirds breed only in relatively larger patches (Bellamy et al. 1996), suggesting that there may be a minimum patch size threshold in which they will breed.

A benefit to identifying thresholds in landscape structure in general, and patch size in particular, is the ability to identify limiting factors by comparing measurements above and below the observed threshold (van der Ree et al. 2004, Huggett 2005). Changes in proximate factors that coincide with changes in behaviors of the species may be related to the ultimate factors that cause a species to be sensitive to landscape structure. Proximate factors that may be related to area sensitivity in songbirds include landscape pattern (e.g., isolation; Radford and Bennett 2004), increased interspecific interactions (e.g., predation and cowbird [*Molothrus* spp.] parasitism; Ambuel and Temple 1983), and decreased resources (e.g., food abundance; Zanette et al. 2000). Patch isolation is known to negatively influence colonization of patches (Blake and Karr 1987, Dunning et al. 1995) and decrease pairing success (Villard et al. 1993, Van Horn et al. 1995). The relation between frequency of cowbird parasitism and patch size appears to be negative with smaller patches exhibiting higher rates of parasitism (Ambuel and Temple 1983, Donovan et al. 1997) but depends on the host species (Tewksbury et al. 2006). The relation between food abundance, specifically arthropods, and patch size also appears to be negative, but influence of the negative effects may differ between ground-foraging and foliage-foraging songbirds (Nour et al. 1998, Zanette et al. 2000).

If an understanding of how an ecological threshold affects population dynamics is needed for conservation and management, accurate estimates of productivity are critical (Anders and Marshall 2005). Most studies searching for ecological thresholds within landscapes have focused on presence, absence, or density of target species (e.g., Jansson and Angelstam 1999, Radford and Bennett 2004, Denoël and Ficetola 2007), which may not be indicative of productivity (Van Horne 1983). Presence of an individual of a territorial species, such as a songbird, in a patch might not signify territory establishment because songbirds explore

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alternative sites before settling (Hildén 1965). Likewise, establishment of territories by individuals may not signify pairing success (Burke and Nol 1998). In many monogamous, territorial songbirds a skewed sex ratio in favor of males will leave some males unpaired (Gibbs and Faaborg 1990). Similarly, pair formation does not always result in productivity (Mayfield 1975).

Our first two objectives were to search for minimum patch size thresholds for presence, territory establishment by males, pairing success, and reproductive success and to verify whether the thresholds for presence, territory establishment by males, or pairing success were indicative of thresholds for reproduction for 2 migratory songbirds that differed in sensitivity to patch size: golden-cheeked warblers (*Dendroica chrysoparia*) and white-eyed vireos (*Vireo griseus*). Golden-cheeked warblers are a federally endangered, neotropical, migratory songbird (U.S. Fish and Wildlife Service 1990) that is considered to be area sensitive based on positive relationships between patch size and abundance, pairing, and productivity (Baccus et al. 2007) and because of lower nesting success near edges (Peak 2007, Reidy et al. 2009). White-eyed vireos are not area sensitive, are known as habitat generalists, and are known to breed in the interior, exterior, and at forest edges (Hopp et al. 1995). Golden-cheeked warblers require mature stands of juniper–oak (*Juniperus* spp.–*Quercus* spp.) forests for breeding (Pulich 1976); white-eyed vireos also breed in juniper–oak forests. Our third objective was to determine whether 2 factors that could potentially limit breeding success, brown-headed cowbird (*Molothrus ater*) parasitism and arthropod biomass, were related to patch size and to compare measurements of each factor above and below the observed thresholds. Both songbirds are susceptible to cowbird parasitism and are insectivorous (Pulich 1976, Hopp et al. 1995). We included white-eyed vireos in the study to compare their responses with that of golden-cheeked warblers and to allow us to determine whether cowbird parasitism was inversely related to patch size in patches below the expected threshold of golden-cheeked warblers. Based on research showing that golden-cheeked warblers are sensitive to patch area and white-eyed vireos are habitat generalists, we predicted that we would find thresholds of reproductive success for golden-cheeked warblers but not for white-eyed vireos. Meeting these objectives could enable resource managers to make decisions about where vegetation clearing should be avoided and where to focus future research and conservation efforts.

STUDY AREA

We conducted our study on private lands in the Cross Timbers and Lampasas Cut Plains of north-central Texas, USA (Hatch 2008). The area (2,880 km^2) consisted of canyons, mesas, and bottomlands composed of alkaline soils and limestone bedrock. Removal of Ashe juniper (*Juniperus ashei*) surrounding juniper–oak forests when combined with fire history, grazing patterns, soil types, and topographic relief resulted in a natural mosaic that included patches of mature juniper–oak woodlands of varying sizes. About 13% of the study area was composed of patches of mixed juniper–oak forests. The remaining area was composed of a mosaic of cropland, nonnative pastures, savanna grasslands, and developed areas.

METHODS

We defined a patch as a stand of mature juniper–oak forest with canopy closure ranging from 35% to 100% that was between 8 m and 40 m from other such patches (Texas Parks and Wildlife 2007). We set the minimum distance at 8 m because gaps in forests as narrow as 8 m produce negative edge effects by attracting brown-headed cowbirds and nest predators to forest edges and within adjacent forests (Rich et al. 1994), which could have direct effects on productivity within forests. In addition, researchers have found that golden-cheeked warbler territories rarely (4 of 66 territories in one study) overlap continuous openings in the forest canopy >8 m across (M. Lackey, Texas A&M University, unpublished data), which suggests that golden-cheeked warblers perceive patches separated by >8-m gaps as distinct patches. We set the maximum distance between patches to approximately 40 m to control for patch isolation. We assessed the amount of juniper–oak forest surrounding the patches to determine whether patch size correlated with the amount of forest in the landscape. White-eyed vireos are known to breed within patches of habitat suitable for golden-cheeked warblers (J. A. Butcher, Texas A&M University, personal observation).

We searched for thresholds in patches that ranged from 2.9 ha to 27.7 ha. The minimum patch size we surveyed represented the approximate mean territory size of golden-cheeked warblers (Pulich 1976). The maximum size exceeded the patch size in which golden-cheeked warblers are known to succeeded (23 ha; K. A. Arnold, Texas A&M University, unpublished report). All available patches of mature juniper–oak forests that existed entirely on accessible private property in Bosque, Coryell, and Hamilton counties made up the sampling frame. We surveyed different patches each year to increase the number of total patches surveyed and decrease the influence of patch-specific covariates not measured.

We used a method developed by Vickery et al. (1992) (hereafter Vickery method) to estimate reproductive activity of birds. The Vickery method alleviates time constraints of locating and monitoring nests while allowing researchers to predict reproductive stage of males and pairs based on behavioral observations, observations of host-species fledglings, and observations of cowbird fledglings (Vickery et al. 1992, Christoferson and Morrison 2001). Males and pairs are assigned ranks that represent the most advanced stage of reproductive activity reached during the season. Ranks included male present (rank 1), territory formation (rank 2), pair formation and fledging cowbird young (rank 3), and fledging host-species young (rank 4). We delineated territories using spot-mapping and conducted fledgling searches until territories began to dissolve. We recorded an average of 41 points per territory over an average of 12 visits per territory, which exceeded recommendations by International Bird Census Committee (1970) for mapping territories. We searched each territory for fledglings an average of 12 times and spent an average of 32 (SE = 0.5) minutes within each territory during each visit.

We collected branch clippings from 22 April to 10 May 2006 and from 24 April to 7 May 2007 as a measure of arthropod abundance (Keane and Morrison 1999). We randomly placed sampling stations by overlaying each study patch with a 100 m × 100 m cell grid that had a random origin, assigning each intersection a number, and using a random number table to select stations. The number of sampling stations was proportional to patch size. We collected branch samples from Ashe juniper and Texas oak (*Quercus buckleyi*) at each station during the peak period of the breeding season in the study area (J. A. Butcher, personal observation).

We analyzed the relations between patch size and number of territories established, number of pairs formed, and number of pairs that fledged ≥ 1 fledgling for each species using Poisson regression (Agresti 1990). Predictor variables included patch size, an indicating factor for songbird species, and an interaction between patch size and species. We compared thresholds of each rank to the threshold of reproductive success to determine whether any of the ranks could be used as an indicator of reproductive success. If the minimum patch size threshold of presence (i.e., the smallest patch in which the species was present) was equal to the minimum patch size threshold of reproductive success (i.e., the smallest patch in which the species successfully fledged young), we concluded that the former was a good indicator of the latter. Similarly, we compared minimum patch size thresholds of territory establishment and pairing success to thresholds of reproductive success.

We analyzed the relationship between patch size and arthropod biomass by calculating Pearson's correlation coefficients (Dowdy and Wearden 1983) to determine whether patch size influenced arthropod biomass. We calculated mean and standard error of arthropod biomass in patches above and below thresholds of reproductive success.

We regressed area of forest surrounding patches on patch area to assess the relation between patch area and area of forest surrounding each patch. We ran regressions for 7 buffers ranging from 100 m to 1,000 m from patches. We calculated the standardized residuals for each regression as measures of area of forest surrounding patches that were independent of patch area. If the standardized residuals were significant, we entered them into a Poisson regression model, which included patch size, the standardized residuals, an indicating factor for songbird species, an interaction between patch size and species, and an interaction between the standardized residuals and species. This model allowed us to determine whether the standardized residuals influenced the response variables given the influence of patch size. We calculated and squared Cramer's Φ to measure how much shared variance was accounted for by each variable in the relationship detected by the Poisson regression (Agresti 1990).

RESULTS

We monitored 24 golden-cheeked warbler and 47 white-eyed vireo territories in 12 patches: 5 patches (range: 2.9–27.7 ha) from 15 March to 6 July 2006 and 7 different patches (range: 3.2–22.2 ha) from 16 March to 26 June 2007. Area of forest surrounding the patches did not help explain number of territories established, number of pairs formed, or number of pairs that fledged ≥ 1 fledgling given patch size (Table 1). We observed golden-cheeked warblers in 11 of 12 (92%) patches including the smallest patch studied (Table 2). Male golden-cheeked warblers established territories in all 11 patches in which they were present and established pairs in 7 (64%) of the patches where they established territories. Pairs fledged young only in patches >15 ha, and no more than one pair formed in any patch ≤ 15 ha. In patches >15 ha, 15 of 17 (88%) males were paired and 13 of 15 pairs (86%) fledged young. In patches ≤ 15 ha, 3 of 7 (42%) males were paired. Despite the presence of brown-headed cowbirds in the patches, we observed no evidence of cowbird parasitism on golden-cheeked warblers.

Male white-eyed vireos established territories in 11 of 12 (92%) patches including the smallest patch studied (Table 2). Pairs formed in 10 of 12 (83%) patches. Pairs fledged young only in patches >4.1 ha. Forty of 45 (88%) males were paired and 27 of 40 (68%) pairs fledged young. In patches ≤ 4.1 ha only 1 of 2 territorial males paired. Two white-eyed vireo pairs fledged cowbird young. One pair was in the 2.9-ha patch and the other was in the 15-ha patch.

We found that Poisson regression models that included patch size, species, and patch size × species fit observed data for all 3 stages of reproductive activity measured: number of territories established (goodness-of-fit $\chi^2 = 12.7$, $P = 0.882$), number of pairs formed (goodness-of-fit $\chi^2 = 20.6$, $P = 0.422$), and number of pairs that fledged ≥ 1 host-species young (goodness-of-fit $\chi^2 = 21.8$, $P = 0.353$; Table 3). Although there were more white-eyed vireos than golden-cheeked warblers in many of the patches, the relation between patch size and the number of territories established (Fig. 1A) and patch size and the number of pairs (Fig. 1B) was similar between species (Table 3). Given species and patch size × species in the model, patch size had a positive relationship with number of territories established (Fig. 1A) and number of pairs formed (Fig. 1B). Excluding area of forest surrounding patches, patch size alone explained 46%, 56%, and 62% of the variability in number of territories established, number of pairs formed, and number of pairs that fledged ≥ 1 host-species young, respectively (Cramer's $\Phi = 0.68$, 0.75, and 0.79, respectively). The relation between patch size and reproductive success, however, differed between species (Table 3). As patch size increased, differences between the numbers of successful pairs decreased (Fig. 1C). The difference in patches <20 ha was due to no golden-cheeked warbler pairs fledging young.

We collected 208 branch clippings each from juniper and oak. Arthropod biomass in Ashe juniper and Texas oak did

Table 1. Effect sizes (square of Cramer's Φ) of each independent variable within 7 buffer distances on 3 dependent variables: number of territories established (Territory), number of pairs (Paired), and number of pairs that fledged ≥1 young (Success) for golden-cheeked warblers and white-eyed vireos breeding in east-central Texas, USA, from 2006 to 2007. Effect sizes represent the proportion of shared variance explained by each independent variable.

Independent variables	Dependent variables	Buffer (m)						
		100	200	300	450	650	800	1,000
Territory	Size	0.46	0.46	0.46	0.46	0.45	0.43	0.40
	Species	0.04	0.04	0.04	0.04	0.04	0.04	0.03
	Surrounding forest	0.11	0.06	0.02	0.00	0.00	0.00	0.01
	Species × size	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Species × surrounding forest	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Paired	Size	0.55	0.56	0.56	0.56	0.55	0.52	0.46
	Species	0.09	0.10	0.10	0.10	0.11	0.12	0.11
	Surrounding forest	0.09	0.04	0.01	0.00	0.00	0.00	0.00
	Species × size	0.01	0.02	0.02	0.02	0.03	0.03	0.02
	Species × surrounding forest	0.00	0.00	0.00	0.01	0.04	0.03	0.01
Success	Size	0.57	0.63	0.62	0.63	0.59	0.52	0.42
	Species	0.18	0.21	0.21	0.21	0.22	0.22	0.20
	Surrounding forest	0.07	0.02	0.00	0.00	0.00	0.00	0.00
	Species × size	0.13	0.15	0.14	0.15	0.17	0.18	0.17
	Species × surrounding forest	0.00	0.00	0.00	0.02	0.10	0.10	0.09

not correlate with patch size ($r = 0.04$, df = 207, $P = 0.574$; $r = 0.002$, df = 207, $P = 0.978$; respectively; Fig. 2A, B). Mean arthropod biomass above the observed threshold was 0.16 mg/g ($n = 4$, SE = 0.04) and 0.50 mg/g ($n = 4$, SE = 0.26) in juniper and oak trees, respectively. Below the observed threshold, the mean arthropod biomass was 0.14 mg/g of leaves ($n = 8$, SE = 0.03) and 0.45 mg/g of leaves ($n = 8$, SE = 0.15) in juniper and oak trees, respectively.

DISCUSSION

We found evidence of a minimum patch size threshold of reproductive success for golden-cheeked warblers between 15.0 ha and 20.1 ha. Presence, territorial establishment, and pairing success were not reliable indicators of the absence of production below 20 ha. Researchers studying golden-cheeked warblers in other parts of their range found that patch size did not affect presence of golden-cheeked warblers (R. H. Benson, Texas Parks and Wildlife, unpublished report), but that golden-cheeked warblers reliably produced young only in patches >23 ha (K. A. Arnold, unpublished report). We failed to find a threshold for white-eyed vireos, which supports the hypothesis that population changes in generalist species that use both edges and interiors is accounted for by amount of habitat rather than fragmentation and patch sizes (Bender et al. 1998).

Importance of small patches to population stability and growth is likely significant for golden-cheeked warblers because the landscape in which they have historically bred was naturally patchy (Pulich 1976). Small patches may be important for movements along migratory paths (e.g., stopover sites), for foraging outside of territories, and for intraspecific interactions during the breeding season. Studies have shown that both sexes move outside of breeding territories to assess other genetic partners (Webster et al. 2001), assess reproductive success (Greenwood and Harvey 1982), and for extra-pair mating (Bollinger and Gavin 1991).

Table 2. Presence (Y = yes) and number of golden-cheeked warbler and white-eyed vireo males breeding in east-central Texas, USA, from 2006 to 2007 that reached each level of reproductive activity based on measurements using the Vickery method (Vickery et al. 1992). We made observations in 12 patches ranging from 2.9 ha to 27.7 ha. Threshold of reproductive success observed for golden-cheeked warbler (dashed line).

Patch size (ha)	Golden-cheeked warbler				White-eyed vireo			
	Present[a]	Territorial[b]	Paired[c]	Successful[d]	Present[a]	Territorial[b]	Paired[c]	Successful[d]
27.7	Y	6	5	5	Y	9	9	6
22.2	Y	3	3	3	Y	6	6	4
21.1	Y	4	3	2	Y	10	9	6
20.1	Y	4	4	3	Y	7	5	3
15.0	- - - - - -	- - - - - - -	- - - - - -	- - - - - - -	Y	2	1	
11.9	Y	1			Y	4	4	4
10.8	Y	1	1		Y	2	1	
8.9	Y	1			Y	3	3	2
4.4	Y	1	1		Y	2	2	2
4.1	Y	1	1					
3.2	Y	1			Y	1	1	
2.9	Y	1			Y	1		

[a] Observed individual in the patch during the breeding season.

[b] No. of males that established and defended a territory for >4 weeks.

[c] No. of males observed with a female for >4 weeks.

[d] No. of pairs that successfully fledged ≥1 offspring.

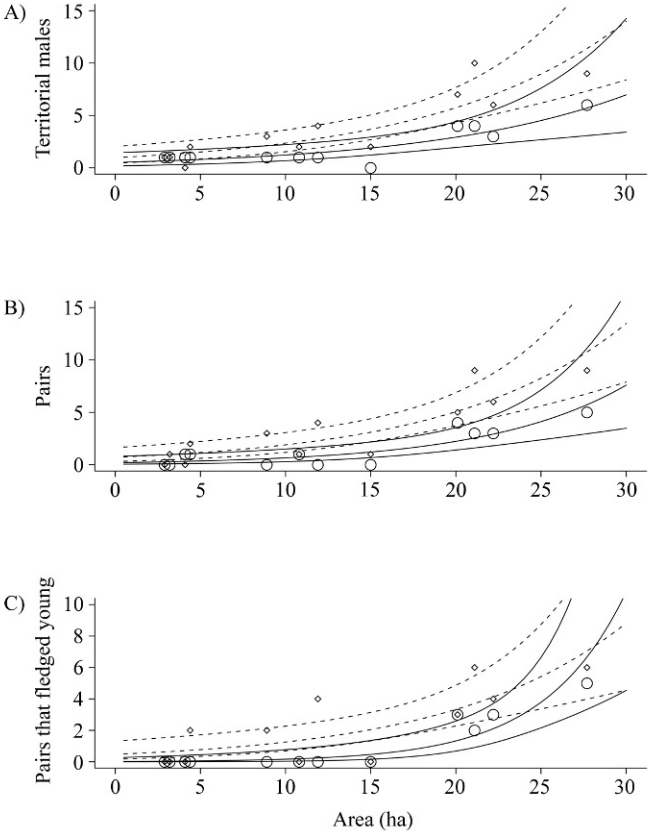

Figure 1. Poisson regressions relating patch size to the number of golden-cheeked warblers (open circles and solid lines) and white-eyed vireos (solid diamonds and dotted lines) breeding in east-central Texas, USA, from 2006 to 2007 that achieved each stage of reproduction: (A) territory establishment, (B) pair formation, and (C) reproductive success. Bold lines represent means; plain lines represent upper and lower 90% confidence limits.

Although research has shown that birds nesting in smaller patches experience higher parasitism (Hoover et al. 1995), parasitism was not a proximate cause for the apparent threshold we observed. Low parasitism frequency was surprising because of the ubiquity of brown-headed cowbirds in our study area. Cowbirds were observed at 88% of survey stations within the region (Juarez Berrios 2005), and >80% of black-capped vireo (*Vireo atricapilla*) and white-eyed vireo nests in shrubs and trees surrounding our study patches were parasitized by brown-headed cowbirds (Farrell 2007).

We did not find evidence of a relationship between patch size and arthropod biomass nor did we observe a difference between arthropod biomass above and below the possible threshold. Canopy-dwelling arthropods available to songbirds do not appear to be affected by patch size (Nour et al. 1998, Buehler et al. 2002). There are indications, however, that availability of soil-dwelling arthropods can become a limiting factor for some songbirds as patch size decreases (Burke and Nol 1998, Zanette et al. 2000). Van Wilgenburg et al. (2001) reported that soil-dwelling arthropods responded negatively to edge effects, whereas canopy-dwelling arthropods in the same forests showed no response to edge, which could explain why we found no relationship with patch size.

Apart from patch size, landscape structure (i.e., isolation, forest surrounding patches) may affect occupancy (Fahrig and Merriam 1994, Magness et al. 2006) and nesting success in birds (Robinson et al. 1995, Donovan et al. 1997). A positive correlation between patch size and area of forest surrounding the patch could obscure the relation between patch size and occupancy (Gustafson and Parker 1992). We controlled for patch isolation in our methods, and the lack of a relation between area of forest surrounding each patch and territory establishment, pair formation, or reproductive success suggests that area of forest surrounding each patch did not influence the results.

The importance of small patches in local source-sink dynamics (Pulliam 1988) and metapopulations (Levins 1970) is unknown and all too often ignored. Reproduction in small patches of habitat may play an important role in conservation of species that live in patchy environments. Identifying minimum patch size thresholds of reproductive success could help place biologically important spatial boundaries on conservation efforts. If research is only focused on larger patches, incorrect conclusions about population dynamics are likely to be made. Although it is possible that small patches may act as ecological traps (Battin 2004), discounting such patches simply because of this possibility would be unwise. Patches of suitable habitat that are not large enough to maintain viable populations without emigration from outside sources may contribute to overall regional population viability if reproduction occurs at replacement levels in some years within the patches (Howe et al. 1991).

Table 3. Poisson regressions models describing the relations between patch size and species and three stages of reproductive activity for golden-cheeked warblers and white-eyed vireos breeding in east-central Texas, USA, from 2006 to 2007.

	No. of territories established				**No. of pairs formed**				**No. of pairs that fledged ≥1 young**			
			90% CI				**90% CI**				**90% CI**	
Parameters	$\hat{\beta}$	**SE**	**Lower**	**Upper**	$\hat{\beta}$	**SE**	**Lower**	**Upper**	$\hat{\beta}$	**SE**	**Lower**	**Upper**
Intercept	−0.666*	0.527	−1.5323	0.2010	−1.647*	0.724	−2.8384	−0.4552	−3.910*	1.315	−6.0725	−1.7478
Size	0.087*	0.026	0.0437	0.1301	0.122*	0.033	0.0674	0.1776	0.210*	0.054	0.1203	0.2990
Species	0.633*	0.650	−0.4354	1.7022	1.307*	0.840	−0.0746	2.6888	3.163*	1.415	0.8363	5.4901
Species × size	0.002*	0.032	−0.0511	0.0553	−0.024*	0.039	−0.0892	0.0403	−0.112*	0.060	−0.2108	−0.0135

* $P < 0.10$.

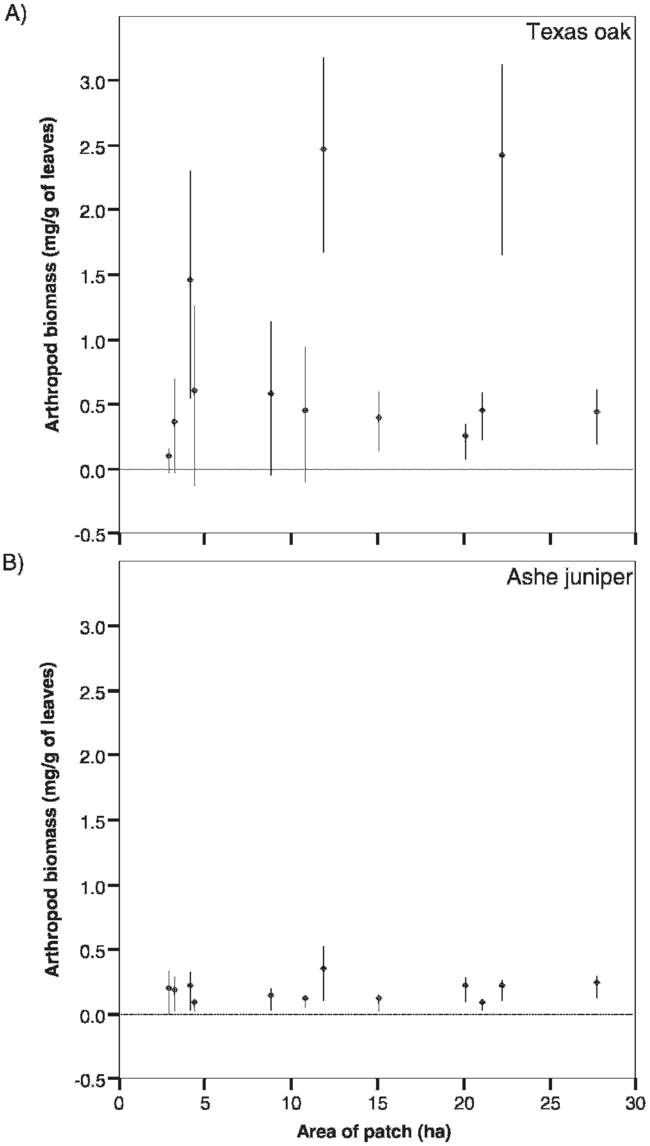

Figure 2. Arthropod biomass in each patch obtained from branch clippings of Ashe juniper (A) and Texas oak (B) during the average nestling and fledgling stages of golden-cheeked warblers and white-eyed vireos in east-central Texas, USA, from 2006 to 2007. Closed circles represent mean arthropod biomass and lines represent 90% confidence intervals.

MANAGEMENT IMPLICATIONS

Managers involved in vegetation clearing in north-central Texas particularly, and across the distribution range of golden-cheeked warblers in general, should be cautious not to decrease patches below 20 ha. Golden-cheeked warblers have relatively uniform habitat requirements across their distribution range (Pulich 1976); therefore, patch size relationships observed in our study should hold across much of their range, although further research to confirm this hypothesis should be conducted. Patches of habitat <20 ha in area may not be large enough to sustain a viable population of golden-cheeked warblers in the long-term; however, such patches may benefit populations if the patches can sustain breeding pairs in the short-term. Research is needed to determine the role that patches <20 ha play in populations of golden-cheeked warblers. Also, the magnitude of difference between cowbird parasitism of white-eyed vireo nests inside and outside of juniper–oak forest patches in our study area suggests a relationship that should be studied.

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